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# Grazing by food-limited microtine rodents on a productive experimental plant community: does the "green desert" exist?

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In many productive terrestrial biomes there seems to be an abundance of forage which is not exploited by herbivores. This observation has generated several hypotheses. One set of hypotheses suggests that the herbivores are either regulated by predators, social interactions or pathogens, and that the abundant plant biomass is an effect of relatively low herbivore densities and a low grazing pressure. The other set claims that the quality of the bulk of the vegetation is persistently too low to give herbivores positive energy or nutrient balance. The herbivores should be critically dependent on high-quality plants or plant organs, but the bulk of the vegetation will remain untouched. The herbivores should thus live in a "green desert". The first set assumes that all plants are edible and of sufficiently high quality, while the second set assumes that plants are generally toxic or of low quality. We have tested this assumption with microtine rodents and productive boreal field layer vegetation in a greenhouse experiment. We found that for three of the studied vole species, *Microtus agrestis*, *Clethrionomys rufocanus*, and *C. glareolus*, the vegetation became severely damaged before the individual voles started to lose weight. On average, 10% of the vegetation remained compared with ungrazed controls. Shoot mortality for toxic tall herbs was almost as high as for corresponding non-toxic species. Toxic species also showed a low ability to recover from damage one year after grazing. Toxicity was thus only marginally successful in protecting plants against grazing. We concluded that the first set of hypotheses thus seemed to be built on a more realistic assumption than the second set. Long-term effects after the grazing had ended showed that herbs generally suffered while grasses were favoured, regardless whether the voles preferred herbs or grasses. This suggests that the graminoid strategy is superior in dealing with pulsatory grazing.

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One of the great mysteries in nature is that, in many productive terrestrial biomes, the world is green (Van Valen 1973): there seems to be an abundance of forage that is not exploited by herbivores but largely goes into the detritus chain. The authors that first discussed this paradox regarded it as evidence for the predation-limitation of herbivores: i.e. predators, rather than food, keep population densities of herbivores down (Hairston et al. 1960; to be referred to as HSS; extensions of the HSS-argument can be found in Fretwell 1977 and Oksanen et al. 1981). Other authors had also made the same observation: Chitty (1960) observed that populations of small herbivorous mammals could decline without any obvious depletion of their food supply (see also Krebs 1964, 1978, Krebs and Myers 1974). Chitty interpreted his observations as evidence for the overwhelming im-

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portance of social factors in the regulation of mammalian herbivore populations.

Many authors have pointed out that the apparent abundance of forage in the world is not adequate evidence against resource-limitation of herbivore populations. Perhaps the quality of the bulk of the vegetation is persistently too low to give herbivores positive energy or nutrient balance (e.g. Murdoch 1966, Myllymäki 1977, White 1978), so that herbivores live in a "green desert" and are critically dependent on relatively rare high-quality plants or plant organs. A similar view is presented by Abe and Higashi (1991) who attribute the "greenness" of the world (especially in forests) to the scarcity of insects capable of breaking down cellulose, which is the primary cell-wall component of higher plants.

These ideas on population regulation of herbivores differ fundamentally in the way they view plant communities and plant-herbivore interactions. The HSS and Chitty hypotheses predict a high standing crop because of low grazing pressure by herbivores on the plant community as a whole, caused by factors external to the plant community: i.e. predators or social interactions among herbivores. All plants are implicitly seen as edible and capable of providing enough energy or nutrients for the herbivores. The "green desert" hypothesis also predicts a high standing crop because of low grazing pressure. However, the grazing pressure on the plant community as a whole is kept low because the plant biomass is either toxic or of low quality to the herbivores. Grazing on high quality plants or plant organs should be intense, and the increase and invasion of fast growing non-toxic plants is prevented both by grazing and by competition from non-grazed low quality plant species (Freeland 1974). Toxicity or low quality of plants should also be maintained over time by selective grazing pressures.

It is possible to test an essential assumption of these hypotheses by allowing microtine rodents to graze in enclosed areas where predation or social interactions cannot occur. The enclosures should be large enough so that the herbivores are not able to quickly deplete the vegetation while subsisting on body reserves. Simultaneously, the enclosures should be small enough to allow a single herbivore to overexploit the vegetation given enough time. The vegetation should be from a productive habitat, since it will then have a potential for building up a high standing crop and can thus be expected to be a "green desert" if food is a limiting factor for the herbivores naturally occurring in the habitat. With this experimental design, it is possible to examine the plant community structure when the herbivore starts to have difficulties in maintaining a positive energy and nutrient balance. According to the HSS and Chitty hypotheses, this should happen when the plant biomass is heavily depleted and the plant community structure is totally changed, whereas according to the "green desert" hypothesis, herbivores should have energetic or nutritional problems after the removal of the most preferred plant species or plant organs, and they should thus cause only a small change in plant community structure.

Below, we report on an experiment that attempts to differentiate between the HSS/Chitty hypotheses and the "green desert" hypothesis with regard to the assumption of the edibility of plants. The main questions were: (1) which are the effects on plant community structure when the rodents start having problems with energy or nutrient balance?, (2) which types of plants can survive a high grazing pressure, and which traits are important? and (3) which implications for food-limitation in vole populations does this have?

## Methods

### Experimental design

Plant-animal interactions can be seen as a two-way process. Herbivores have different food preferences, and will thus have different impacts on a plant community. On the other hand, preference is a relative measure dependent on what the animal has to choose from, and altering the species composition in a plant community may thus influence the feeding behaviour of the herbivore (e.g. Crawley 1983). A comparison of grazing effects between species and/or individuals performed in plots in natural communities might be obscured by spatial heterogeneity. To correct for this, we created an artificial boreal forest floor community in a greenhouse. We excavated 25×25 cm squares from middle boreal field layer vegetation and then constructed "artificial" plant communities by randomly assigning squares to plots. The plant communities thus created retained a large part of the small-scale spatial structure found in natural communities, while also being highly comparable with each other, i.e. large-scale spatial patterns were removed from the plant communities.

The experiment was divided into two runs due to limited space in the greenhouse: a first run testing the effects of four different microtine rodents on the plant community performed in 1986–1987, and a replication of treatments with two vole species (*Microtus agrestis* and *Clethrionomys rufocanus*) performed in 1988–1989.

### The plant community

In both cases, 25×25 cm squares were dug up in late autumn (late November-early December) in 1986 and 1988 respectively from two productive forest sites: Stora Orrberget (64°06'N, 20°03'E; *Geranium-Oxalis-Myrtillus*-type, GOMT; Kalela 1961) and Tavelsjöliden (64°01'N, 20°03'E; *Geranium-Oxalis-Maianthemum-*

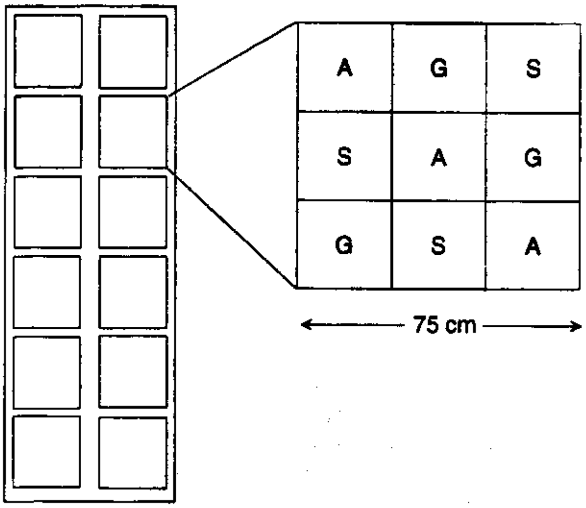

Fig. 1. Experimental design. Each table consisted of twelve blocks of 75×75 cm, and each block was constructed as a 3×3 Latin square design. A stands for *Actaea spicata*, G for *Geranium sylvaticum*, and S for *Solidago virgaurea*.

type, GOMaT; Kalela 1961). The squares were selected according to the following criteria: the first category of squares contained at least one individual of *Geranium sylvaticum* (elevated foliage, non-toxic), the second at least one individual of *Solidago virgaurea* that had flowered during the summer (basal foliage, non-toxic), and the third at least one *Actaea spicata* individual (elevated foliage, toxic; see Appendix), together with all the other species that happened to be growing on the squares. The squares were stored outdoors, covered by snow, until late December 1986 for the first run of the experiment, and until late January 1989 for the second run, when they were taken into the greenhouse. The squares were randomly allocated to 3×3 randomized Latin square blocks (Fig. 1). Twelve randomly chosen blocks were placed on a table covered with 3 cm of coarse gravel in a greenhouse (size of each table: 7.5 $m^2$). The spaces between the blocks were covered with wood to create artificial runways for the rodents which enabled them to reach each block with equal probability. The total vegetated area on each table was approximately 6.75 $m^2$. The available space in the greenhouse allowed for five such tables in each of the two runs of the experiment. To simulate spring conditions for the plants, temperature regime was held at 2–6°C during the first week, raised to 5–10°C during the second week, and then to 10–15°C during the third week. Thereafter temperature was maintained at 15–20°C with maxima going up to 25°C depending on natural light levels. The tables were regularly watered, fertilized with a 0.2% commercial standard fertilizer (Superba T; 3.2% N, 1.0% P, and 4.7% K) every fifth day after the beginning of plant growth, and light regime was L:D 18:6.

## The herbivores

The five tables were randomly allocated to five treatments in 1987 (ungrazed control, grazing by *Microtus agrestis*, *Clethrionomys glareolus*, *C. rufocanus*, and *Lemmus lemmus*, respectively), and three treatments in 1989 (ungrazed control, grazing by *M. agrestis* × 2, and grazing by *C. rufocanus* × 2). On each table, one individual of the respective herbivore species was placed, which gave a sample size of three replicates (three individuals on three different tables) for *M. agrestis*, three replicates for *C. rufocanus*, two control replicates, and unreplicated treatments for *C. glareolus* and *L. lemmus* when both runs of the experiment were combined. Each table was enclosed with a net with 1.2 × 1.2 cm mesh size, and the top of the net was lined with aluminium sheets bent inwards to prevent escape. Four Ugglan special live traps were placed on each table to enable us to capture and weigh each animal.

The experiment was carried out using young female rodents that had not reproduced before the experiment. The *C. rufocanus* individuals were trapped in the autumn before each experimental run in northernmost Norway (Finnmarksvidda; 69°46′N, 24°00′E; altitude 400–600 m a.s.l.). The individual used in 1987 was from an increasing population, whereas the ones used in 1989 were from a declining one (see Oksanen and Oksanen 1992). The *M. agrestis* individuals used in 1989 were from the vicinity of Umeå (i.e. within 25 km from where the plant material was collected), but the individual used in 1987 was from a south Swedish (Scania; 55°42′N, 13°25′E) non-cyclic population (due to a synchronous cyclic low in northern and central Scandinavia, specimens from northern populations could not be obtained). The *C. glareolus* individual was also from the vicinity of Umeå (increasing population), and the *L. lemmus* individuals were from the laboratory colony of the Univ. of Helsinki. The use of animals from different areas than those where the plant material was collected may bias the experiment in favour of the "green desert" hypothesis. However, even though the animals were not adapted to feeding on the exact same plant community used in the experiment, the majority of the plant species are found in the areas where the animals were caught with the exception of the lemmings, and we see this design as a conservative test of the "green desert" hypothesis. The animals were kept in short day length and fed with commercial rabbit pellets until 2 weeks before the experiment, when fresh herbs were added to the diet and the cages were kept in continuous light to simulate spring conditions. Two days before the start of the experiment, the voles were paired with a male to make them pregnant. However, only the *C. rufocanus* individual of 1987 actually developed visible signs of pregnancy (see below). This was an unsuccessful attempt to see if food quality/quantity would be sufficient for the rodents to rear young. As the pairing failed for most individuals, we only discuss individual adult survival of the rodents, and the effects of food resources on reproduction and population dynamics was not tested.

## Sampling

Before the animals were released on the tables, all emerging plant shoots on six randomly chosen blocks on each table were marked with coloured plastic ribbons and counted. For grasses, individual tillers were marked with ink (hereafter included under "shoots"). The marked shoots were censused once a week for the first three weeks, and then once every second week until the experiment ended. Newly emerged shoots at each census were marked with different colours to enable us to distinguish different cohorts. Flowering shoots and seedlings were counted as separate categories from vegetative shoots. Each shoot was noted as either surviving, withered or eaten. A shoot was regarded as eaten if less than an estimated 5% of its photosynthetic tissue remained. A total of 25511 shoots were marked in 1987, and 28372 in 1989, giving a grand total of 53883 shoots of 53 vascular plant species marked and censused in the experiment.

The voles were introduced into the enclosures when the phenological situation corresponded to early summer (*Actaea spicata* and *Maianthemum bifolium* beginning to flower), i.e. 10 February in 1987 and 14 March in 1989. The voles were trapped and weighed every second day. Our goal was to terminate the experiment when the body weight data indicated a nutritional stress. In the cases where weight loss and/or death was unexpectedly fast (*L. lemmus*) or depended on accidentally closed traps (*C. rufocanus* in 1989), a new individual was put in to see if it would have the same weight trend as the first individual. In 1987, we terminated the experiment on 22 March when the *C. rufocanus* individual escaped from the enclosure after a period of declining body weights. At that date, the weight of the *M. agrestis* individual had also declined below the initial level. In 1989, the *C. rufocanus* experiment was terminated after one individual had escaped and died in a trap and the other died accidentally in a closed trap on the table. Since the new individuals that were put in on both tables showed signs of losing weight we decided to terminate the *C. rufocanus* treatments on 24 April. As the *M. agrestis* individuals showed no signs of nutritional stress, those treatments were continued until the temperatures in the greenhouse reached unnaturally high levels at 6 June.

After the voles were removed from the tables, the above-ground shoots on the censused blocks in 1987 (n = 6), and on all blocks in 1989 (n = 12), were harvested, sorted by species, dried at 40°C for 72 h and weighed. To have an appropriate control for each treatment in 1989, we harvested six randomly chosen blocks on the control table on 24 April (three with marked shoots and three without; referred to as "early control"), and the remaining six on 6 June (referred to as "late control").

## Long-term effects

To evaluate the long-term effects of the grazing treatments on plant biomass, the remaining six blocks on each table that were not harvested in 1987 were replanted in open soil in an experimental garden outside the greenhouse in late April 1987. They were left to grow until 21 June, 1988, and then harvested in the same way as described above. The harvest date were set phenologically as when *Geranium sylvaticum* were in full flower. The plants were thus allowed to recover during one growing season, and to build up shoot biomass in the subsequent growing season.

## Data analyses

Preferences for the different rodent species were calculated based on the number of cut shoots in each treatment during the first week by Jacob's forage ratio ($E_i$; Jenkins 1979, Lechowicz 1982):

$$E_i = \ln \left( \frac{r_i(1-p_i)}{p_i(1-r_i)} \right)$$

where $r_i$ is the proportion of shoots cut of species $i$, and $p_i$ is the proportion of shoots available belonging to species $i$. A forage ratio greater than 0 implies preference for a species, and a ratio smaller than 0 implies avoidance. We used the number of cut shoots during the first week as a measure of preference since that was the only period when food options would not be substantially influenced by past consumption. Significance of each $E_i$ was tested by computing:

$$X^2 = \frac{E_i^2}{\left( \frac{1}{X_i} + \frac{1}{(m-X_i)} + \frac{1}{Y_i} + \frac{1}{(n-Y_i)} \right)}$$

where $x_i$ and $y_i$ are the number of shoots cut and available, respectively, of species $i$, and $m$ and $n$ are the total number of shoots cut and available, respectively. $X^2$ was compared with a Chi-square distribution with one degree of freedom (Jenkins 1979). Plant species with less than 10 shoots on a table, or which were neither significantly preferred nor avoided, have been deleted from Table 2 for clarity, although they were included in the computation of the indices since they were available as food for the rodents.

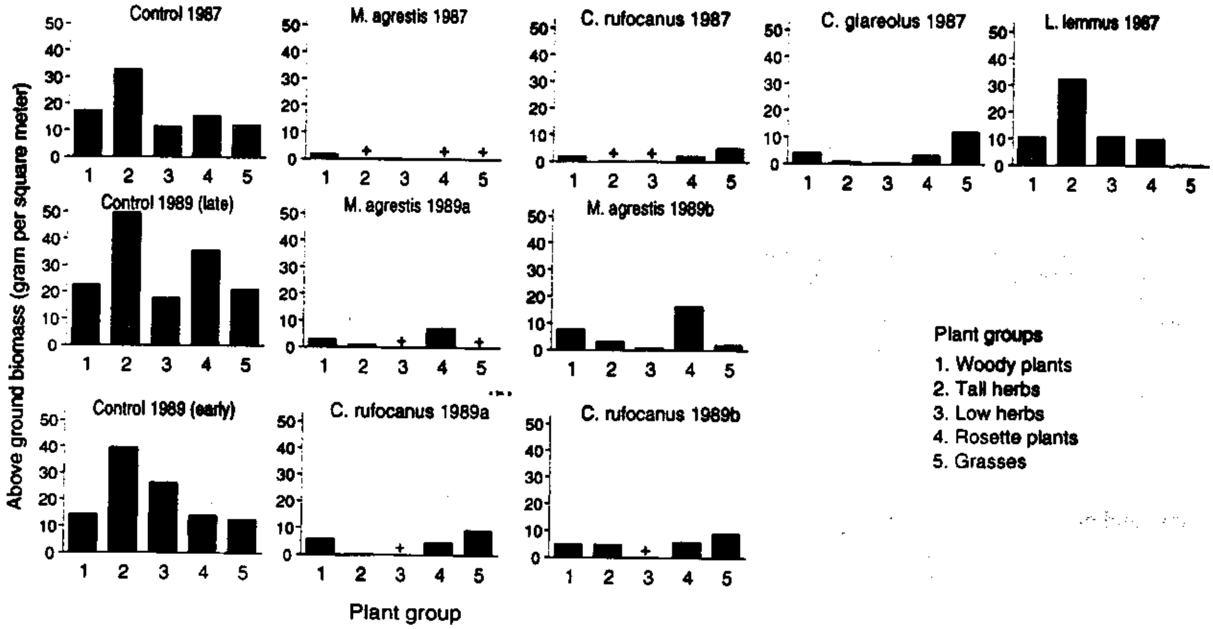

Fig. 2. The above-ground biomass at the end of the experiment measured as g dry weight per m$^2$. A "+" denotes small amounts, not visible on the graph. Each vole treatment should be compared with the control at the left on the same row.

The changes in community composition over time in the treatments were examined with a detrended correspondence analysis (Jongman et al. 1987). The number of shoots of the different plant species on each table and at each census was used as samples, and samples belonging to the same table were connected in the plot to give a visual picture of the community changes occurring over time. Only data for species present on all tables were used in order to remove the influence of rare species.

The harvested plant species were pooled for each table and divided into woody plants, tall herbs, low herbs, rosette plants and grasses (see Appendix). The rosette plant group is somewhat heterogeneous since both graminoids (*Luzula pilosa* and *Carex* spp.) and herbs were included. Most of the biomass in the group consisted of *L. pilosa* and *Solidago virgaurea*, the rest of the species were fairly rare. We regarded the graminoids as sufficiently different from the grasses, e.g. less silica in the leaves, to warrant the inclusion of the species in the rosette group instead of the grass group. The treatments were tested against the three controls (1987 control, early and late 1989 control) for each plant group with two-sample t-tests (df = 4) for *M. agrestis* and *C. rufocanus*, and with one-sample t-tests (df = 2) for *C. glareolus* and *L. lemmus*. Using treatments and controls from different years as replicates will obscure any differences in the vegetation due to temporal variation, but it will also provide a conservative test where the differences found will reflect grazing effects in the experiment.

The long-term grazing effects on the plants were tested on the blocks planted in open soil after the experiment in 1987. The treatments were tested with ANOVA with blocks as replicates (n = 6). Since the question was how the plants responded to intense graz-

Table 1. Tests of differences between treatments and controls in final biomass of different plant groups. *M. agrestis* and *C. rufocanus* were tested with two-sample t-tests (df=4), and *C. glareolus* and *L. lemmus* with one-sample t-tests (df=2). A star denotes a significant t-value at p=0.05, and two stars denotes a significant t-value with p=0.01.

| Plant group | *Microtus agrestis* | *Clethrionomys rufocanus* | *Clethrionomys glareolus* | *Lemmus lemmus* |
|---|---|---|---|---|
| Woody plants | 4.55 ** | 5.12 ** | 5.63 * | 3.07 ns |
| Tall herbs | 7.82 * | 7.55 ** | 8.07 * | 1.67 ns |
| Low herbs | 4.25 * | 4.30 * | 4.23 * | 1.80 ns |
| Rosette plants | 1.62 ns | 2.42 ns | 2.58 ns | 1.65 ns |
| Grasses | 4.75 * | 2.29 ns | 1.11 ns | 4.95 * |

ns
**

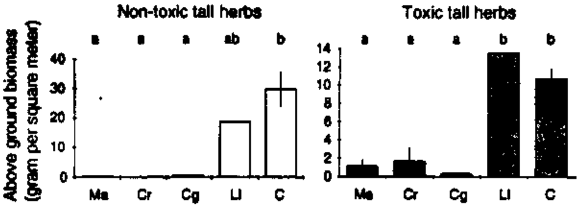

Fig. 3. The above-ground biomass at the end of the experiment of non-toxic and toxic tall herbs. The columns represent average (±SE) biomass (g dry weight per m$^2$) for the three replicates of *Microtus agrestis* (Ma), *Clethrionomys rufocanus* (Cr), and the controls (C). For *Clethrionomys glareolus* (Cg) and *Lemmus lemmus* (Ll) the columns show the biomass from the single 1987 tables. The means are compared with an ANOVA and a Tukey multiple comparison test. Columns with the same letter are not significantly different from each other ($p>0.05$). Non-toxic: $F_{4,6} = 13.2$, $p = 0.004$, Toxic: $F_{4,6} = 15.5$, $p = 0.003$.

ing, and not what the preferences were for each rodent, the blocks were a proper unit for replication, and they were not pooled for each table.

# Results

## Plant biomass

Most treatments had a large impact on plant biomass (Fig. 2). The only exception was *L. lemmus* which only significantly reduced the grasses (Table 1). *M. agrestis* had a significant impact on all plant groups except rosette plants, while the *Clethrionomys* individuals had strong impacts on woody plant and herb biomass. Rosette plants did not experience a significantly lower biomass in any treatment. Grasses were significantly depleted by *M. agrestis* and *L. lemmus*, but not by the *Clethrionomys* individuals.

Toxic tall herbs (*Actaea spicata*, *Convallaria majalis* and *Paris quadrifolia*) had significantly lower biomass than in the controls in all treatments except for the *L. lemmus* treatment (Fig. 3). However, non-toxic tall herbs were more severely depleted than toxic herbs in all vole treatments, i.e. they had a lower biomass in relation to the biomass in the controls than the toxic tall herbs (Fig. 3).

## Long-term effects

The biomass in most plant groups was still depressed one and a half growing seasons after the grazing treatments were terminated (Fig. 4). The grasses, however, showed a different pattern. In both the *M. agrestis* and *C. rufocanus* treatments the grasses had a higher biomass than the control (Fig. 4). The ANOVA was significant ($F = 3.24$, $p = 0.03$), even though the Tukey test did not indicate any differences between the means. This is possible since the ANOVA has a higher power than the Tukey test (Zar 1984). In the other two treatments (*L. lemmus* and *C. glareolus*), the grasses had about the same biomass as the control, although the grass biomass in the *L. lemmus* treatment was significantly lower than in the control directly after the exper-

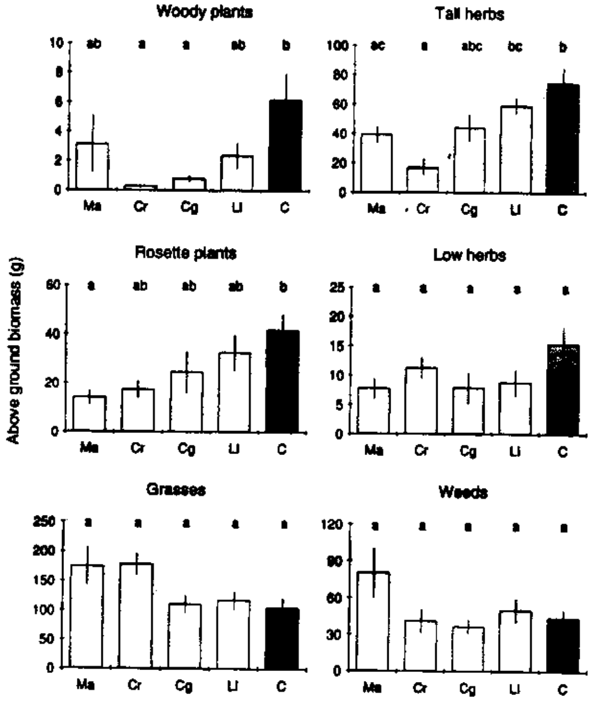

Fig. 4. Long-term effects. The above-ground biomass one growing season after the experiment in 1987. The columns show average (±SE) biomass (g dry weight per block; ca 0.56 m$^2$). The means are compared with an ANOVA and a Tukey multiple comparison test. Columns with the same letter are not significantly different from each other ($p>0.05$). Ma = *Microtus agrestis*, Cr = *Clethrionomys rufocanus*, Cg = *Clethrionomys glareolus*, Ll = *Lemmus lemmus*, and C = Control. Species categorised as weeds do not naturally occur in the studied vegetation.

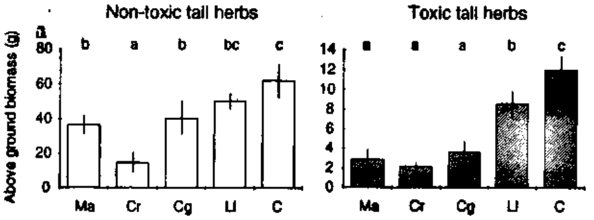

Fig. 5. Long-term effects. The above-ground biomass one growing season after the experiment in 1987 for non-toxic and toxic tall herbs. The columns show average (±SE) biomass (g dry weight per block; ca 0.56 m$^2$). The means are compared with an ANOVA and a Tukey multiple comparison test. Columns with the same letter are not significantly different from each other ($p>0.05$). Non-toxic: $F_{4,25} = 5.68$, $p = 0.002$; Toxic: $F_{4,25} = 14.6$, $p<0.001$.

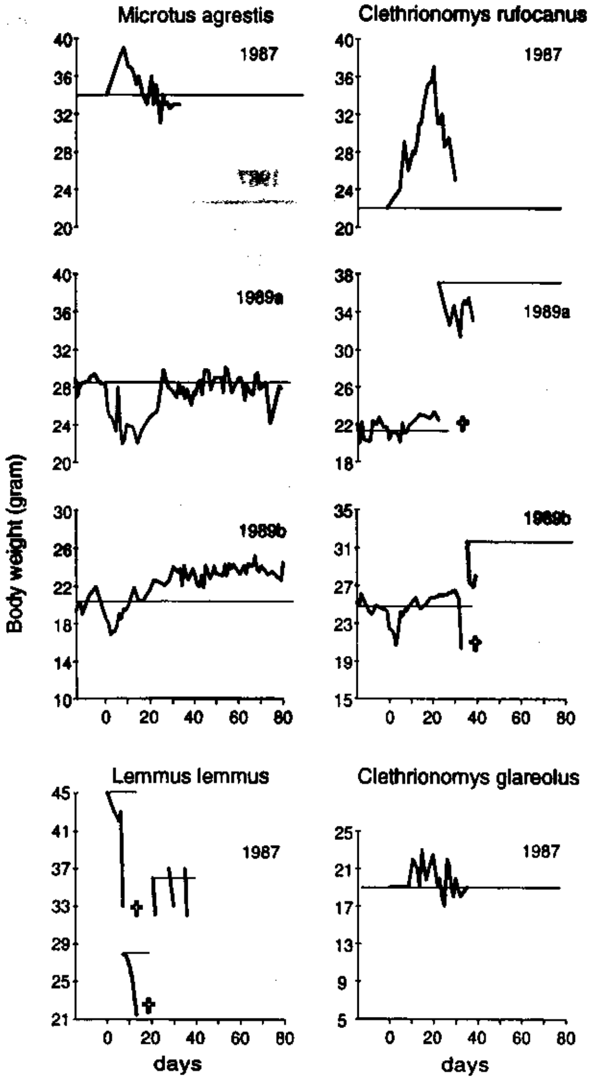

Fig. 6. The body weight of the rodents during the experiment. The thin line shows the weight at the time of release on the tables for the 1987 voles, and the mean weight during the 14 d before the release for the 1989 voles. A cross indicates the death of an individual. See text for details.

iment (Table 1). Toxic tall herbs had consistently lower biomass in vole treatments than in controls or in the lemming treatment (Fig. 5). A large number of weeds (old-field plant species initially absent from the plots) invaded all plots (Fig. 4). Although no statistically significant differences existed between treatments, the data suggests that the *Microtus* treatment was the one that was most sensitive to the invasion of alien plants.

## The rodents

Food-limitation may have been the case for the *C. rufocanus* individuals at the end of the experiment (Fig. 6). The two individuals used in 1989 both died in closed traps after a negative weight trend, and the two new individuals that were immediately placed on the tables both showed a strong negative weight trend. The escape by one individual could have been caused by a strong motivation to escape due to lack of food. The individual used in 1987 clearly was pregnant and, judged on the basis of vaginal development, did give birth to a litter when the weight trend changed half-way through the experiment. However, the young were never found, and were either born dead or died in a nest located in the plots that were to be transplanted and thus could not be inspected. The negative trend in the latter half of the experiment could be due both to giving birth and to food shortage.

The three *M. agrestis* individuals did not show any obvious signs of food-limitation (Fig. 6). The individual used in 1987 showed a somewhat similar trend to the pregnant *C. rufocanus*, and it is possible that it resorbed its litter at an early stage of the experiment.

The *C. glareolus* individual showed no signs of pregnancy or food-limitation (Fig. 6). The *L. lemmus* individual rapidly lost weight and died. A new individual was put in, which also rapidly lost weight and died. After that, a new individual was put in for only one day once a week to maintain the effects of lemming grazing on the vegetation, without causing any further lemming mortality, until the experiment was ended.

## Preferences

Preferences of the different rodent individuals are shown in Table 2. Grasses ranked high in the food choice for *M. agrestis*, and *L. lemmus*, while the two *Clethrionomys* species preferred herbs and avoided grasses. Seedlings seemed to be little used, except by *L. lemmus*. Individual differences within vole species were also apparent, e.g. one *C. rufocanus* individual preferred *Actaea* (toxic species; individual no. 1987), another was indifferent (no. 1989a), and the third avoided it (no. 1989b; Table 2).

Preference indices for pooled data of different growth forms show that grasses were preferred by all three *M. agrestis* individuals, while low herbs were preferred by two (no. 1989:a and 1989:b) and rosette plants were preferred by the third (no. 1987; Table 3). Woody plants and tall herbs were avoided by all. Tall herbs and low herbs were preferred by *C. rufocanus*, while woody plants, rosette plants and grasses were avoided (Table 3).

## Community changes over time

Consistent patterns caused by individuals of the same species, and major differences between species, emerge when changes in abundances on the tables are examined

Table 2. Preferences of the rodent individuals measured as shoot mortality during the first week. The index is Jacob's forage ratio. Significant indices are marked with bold lettering. A star means that there was no shoot mortality and an index could not be calculated. Only indices for species with more than 10 shoots on the table are shown. An "S" in the species columns after the species name denotes seedlings. Only species which are significant in at least one of the tables in each treatment are presented.

| *Microtus agrestis* | | | | *Clethrionomys rufocanus* | | | | *Clethrionomys glareolus* | | *Lemmus lemmus* | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1987 | 1989a | 1989b | | 1987 | 1989a | 1989b | | 1987 | | 1987 |
| melica | **0.380** | **0.868** | **1.062** | geranium | **0.982** | **1.253** | **1.352** | maianthemum | **1.117** | desch flex | **0.913** |
| milium | 0.360 | **1.153** | **0.775** | equisetum | | **1.122** | | melampyrum | **0.996** | luzula S | **0.832** |
| desch flex | **0.387** | **1.356** | **0.493** | pyrola | **0.809** | | **1.035** | convallaria | **0.989** | poa nem | **0.810** |
| melampyrum | 0.284 | **1.392** | 0.494 | maianthemum | –0.140 | **1.353** | **1.269** | pyrola | **0.927** | melica S | **0.774** |
| carex dig | 0.360 | * | **0.957** | viola | 0.293 | **1.193** | | orthilia | **0.903** | luzula | **0.707** |
| agrostis | **0.318** | **0.822** | 0.334 | oxalis | 0.268 | –0.010 | **0.971** | viola | **0.823** | agrostis | **0.678** |
| maianthemum | **–0.451** | **0.670** | **1.249** | gymnocarpium | **0.890** | **0.287** | **–0.485** | geranium | **0.454** | maianthemum | **0.614** |
| oxalis | **0.369** | –0.250 | **0.871** | vacc vit | **0.462** | –0.524 | 0.162 | oxalis | **0.410** | oxalis | **–0.367** |
| trientalis | 0.128 | **0.648** | 0.053 | orthilia | **0.641** | –1.170 | 0.134 | gymnocarpium | **0.282** | vacc myrt | **–0.597** |
| geranium | –0.132 | **–0.425** | –0.159 | actaea | **0.830** | –0.520 | **–0.930** | actaea | **–0.773** | gymnocarpium | **–0.731** |
| vacc vit | **–0.741** | –0.321 | –0.136 | vacc myrt | **0.590** | 0.365 | **–1.658** | solidago | **–0.917** | vacc vit | **–0.958** |
| luzula | **0.338** | –0.198 | **–1.532** | paris | **1.023** | **–0.869** | –1.257 | solidago S | **–0.972** | solidago | **–1.155** |
| luzula S | **0.341** | **–0.937** | **–0.860** | solidago | 0.293 | **–1.042** | * | melica | **–1.356** | linnaea | **–1.233** |
| gymnocarpium | **–0.737** | **–0.355** | **–0.821** | luzula | **–1.058** | **–1.021** | **–0.799** | desch flex | **–5.386** | veronica | **–1.325** |
| linnaea | **–0.415** | **–1.150** | **–0.570** | oxalis S | **–1.597** | | –0.351 | agrostis | * | geranium | **–1.510** |
| actaea | **–0.883** | –0.396 | **–0.995** | linnaea | **–1.217** | **–1.521** | **–0.300** | desch cesp | * | paris | **–1.648** |
| viola | **–1.204** | | –0.460 | melica | **–0.950** | **–1.363** | **–1.570** | lycopodium | * | oxalis S | **–1.665** |
| solidago S | **–0.851** | –0.869 | * | solidago S | **–1.298** | * | * | milium | * | sorbus | **–2.149** |
| vacc myrt | **–0.444** | **–0.759** | **–1.568** | luzula S | **–0.770** | **–1.725** | **–1.400** | | | actaea | **–2.161** |
| paris | –0.405 | –1.606 | **–1.124** | lycopodium | **–1.483** | * | * | | | rubus sax | **–2.426** |
| solidago | **0.345** | **–2.657** | –0.926 | desch cesp | **–1.774** | * | * | | | solidago S | **–2.549** |
| lycopodium | –0.743 | **–1.356** | **–1.830** | agrostis | **–0.916** | * | **–2.640** | | | | |
| athyrium | | | * | melica S | **–2.188** | * | * | | | | |
| desch cesp | | | * | desch flex | **–4.403** | * | **–1.831** | | | | |
| | | | | anthriscus S | * | | | | | | |
| | | | | calamagrostis | * | | | | | | |
| | | | | carex dig | * | | * | | | | |
| | | | | milium S | | * | | | | | |
| | | | | poa nem | * | | | | | | |

(Fig. 7). The plant communities in all four *Clethrionomys* treatments showed an increased abundance of grasses over herbs (Fig. 7). The effect of putting in a new individual in each of the two *C. rufocanus* treatments at the end of the experiment in 1989 did not seem to cause the plant community structure to change in a new direction, i.e. the trends near the end of those arrows were roughly the same as for the *Clethrionomys* treatments in 1987. The endpoint of *Microtus* treatments roughly corresponded to the location of the rosette herb *Solidago virgaurea* (Fig. 7) which was indeed the dominant species at the end of the *Microtus* treatments in 1989. The controls changed only slightly indicating that the normal phenological changes in the vegetation were only a minor component in the changes observed in the treatments. The *L. lemmus* treatment caused an initial reduction in grasses similar to *M. agrestis*, and the effects seemed to be maintained by letting one individual graze for one day a week.

Table 3. Preferences of different plant groups measured as pooled shoot mortality during the first week. All values significant at $p<0.05$ except those marked as ns.

| Individual | Woody plants | Tall herbs | Low herbs | Rosette plants | Grasses |
|---|---|---|---|---|---|
| *Microtus agrestis* | | | | | |
| 1987 | –0.539 | –0.270 | –0.251 | 0.238 | 0.513 |
| 1989:a | –1.083 | –0.570 | 0.236 | –0.752 | 1.247 |
| 1989:b | –0.821 | –0.474 | 0.590 | –0.967 | 0.579 |
| *Clethrionomys rufocanus* | | | | | |
| 1987 | –0.339 | 1.009 | 0.306 | –0.566 | –1.751 |
| 1989:a | –1.021 | 0.961 | 1.013 | –1.349 | –2.304 |
| 1989:b | –0.537 | 0.998 | 0.754 | –1.215 | –1.921 |
| *Lemmus lemmus* | –0.980 | –1.540 | –0.130ns | 0.272 | 0.946 |
| *Clethrionomys glareolus* | –0.135 | 0.269 | 1.221 | –0.447 | –2.687 |

## Discussion

According to the "green desert" hypothesis, the herbivores should deplete their most preferred food plants or plant organs and then start to lose weight. The preferences is thus of high importance: herbivores adapted to different food plants would be expected to experience different plant communities as "green deserts".

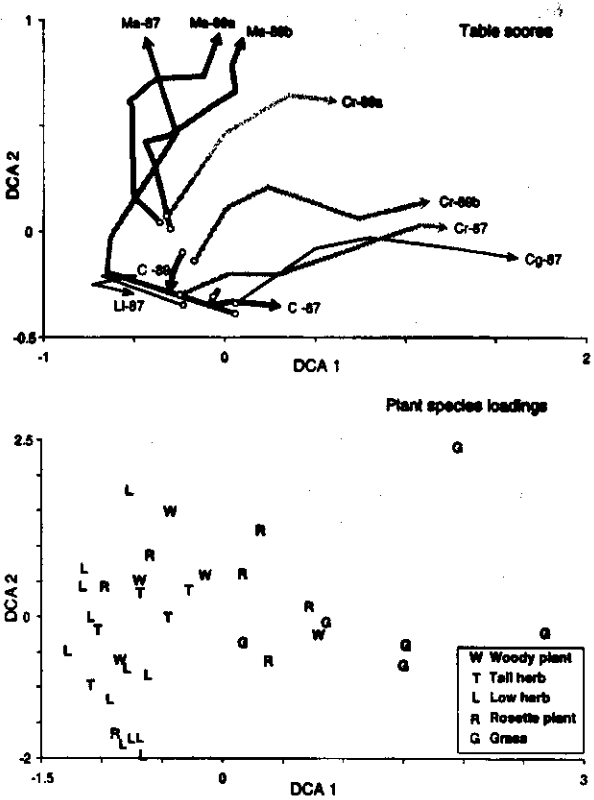

Fig. 7. Detrended correspondence analysis used to show changes in community composition over time. The objects used in the analysis are the shoot number at a given census on a table. The objects for each table are connected on the score plot (top) with a line starting at the open ring (the start of the experiment) and ending with the arrow (the end of the experiment). The control tables are connected with black thick lines, the *M. agrestis* (Ma) tables with dark grey lines, the *C. rufocanus* (Cr) tables with light grey lines, and the *C. glareolus* (Cg) and *L. lemmus* (Ll) tables with thin black lines. On the loadings plot (bottom), individual plant species belonging to the same plant group are represented by the same character.

However, the key point in deciding whether or not a specific plant community is a "green desert" for a specific herbivore is whether the plant community largely retains the same structure after intense unrestrained grazing or not.

The vegetation was severely depleted, and the plant community structure was totally different from the controls, at the end of the experiment in all grazing treatments except for the *L. lemmus* individual (Figs 2 and 7). The voles all survived more than a month in spite of the extremely high grazing pressure on the tables (in the case of *M. agrestis* in 1989, more than 2.5 months). The *M. agrestis* individuals in 1989 and the *C. glareolus* individual had no evident negative weight trends even at the end of the experiment (Fig. 6) despite a significantly lower plant biomass on the tables (Fig. 2). Feeding trials where *Microtus* species (*Microtus oeconomus* and *M. miurus*) have been fed palatable and unpalatable plant species have shown that individuals fed with slightly palatable or unpalatable plants lose body mass rapidly and may even die within one day (Batzli and Lesieutre 1991). The relatively small body mass changes that we observed during the experiment thus means that the plant community provided sufficient food for the voles (see below for discussion on cut versus ingested shoots). The relative abundances of the plant groups were totally changed when compared with the controls at the end of the experiment in all vole treatments (compare the plots in Fig. 2), which leads us to conclude that this plant community was not a "green desert" for the voles.

However, the *L. lemmus* individual rapidly depleted the grasses, together with *Luzula pilosa*, on the table and then lost weight so fast that it was not possible to prevent its death. By putting in new individuals, we were able to show that food, rather than disease or physiological factors, was a probable cause of the negative weight trend since all the other lemmings also lost weight. The plant community used in this experiment was dominated by herbs, and the lemming grazing thus did not change the appearance of the plant community (grasses were the only group with a significantly lower biomass as compared with the controls) and it still appeared green. This type of plant community obviously was a "green desert" for *L. lemmus*, which is not normally found in such habitats. This result shows that it was possible to detect "green deserts" with our experimental design: the animal could not graze down a plant community consisting of plants unsuitable as forage.

For the *Clethrionomys* species, the plant community may have become a "green desert" when all dicots had been depleted and only grasses and rosette plants were left (Fig. 6, Table 1). In the case of *M. agrestis*, we did not get any direct evidence of the existence of a "green desert" at all in this plant community.

The normal vole community of nutrient-rich middle boreal habitats consists of *M. agrestis*, *C. glareolus*, and *C. rufocanus* (Henttonen et al. 1977, Hörnfeldt 1978), and, as this study shows, they are potentially capable of totally changing the structure and appearence of the plant community, although this potential is seldom if ever realized in natural conditions. We conclude that this indicates that the HSS and Chitty hypotheses are built on a more realistic assumption on the edibility of plants than the "green desert" hypothesis, and we suggest that tests of population regulation of microtine rodents in productive habitats should look at hypotheses which predict that factors external to the plants themselves, i.e. predation, disease or social interactions, are important.

## Grazing effects on the plant community

Toxicity was only a marginal success for the plants possessing it. The proportion of biomass of toxic tall herbs were higher in the treatments compared to the controls than for non-toxic tall herbs, but toxic tall herbs were still severely depleted. Thus, it does not seem to be possible to prevent heavy shoot mortality by having a toxin-based defence when vertebrate herbivores are facing food-shortage. In the long run, toxic plants fared even worse than non-toxic: their recovery was slower than that of the non-toxic tall herbs one growing season after the vole grazing had terminated (Fig. 5). Thus, toxic species, in spite of facing lower biomass losses compared with non-toxic species, suffer more in the long run. This suggests that toxicity in forest floor herbs seems to coincide with an inferior ability to recover from damage (cf. Ericson and Oksanen 1987).

Regardless whether the voles preferred herbs or grasses, herbs were damaged in the long-run while grasses were favoured, especially in the *M. agrestis* and *C. rufocanus* treatments where total impact on the vegetation was strong (Figs 2 and 4). Grasses have their meristems protected close to the ground, which tend to make them less sensitive to grazing compared to herbs. This also enabled them to take advantage of the open space on the blocks created by the foraging of the herbivores, and to increase rapidly when the grazing had ceased. They thus have an initial advantage in shoot competition in situations where grazing is intermittent, and this probably persists for quite a long time until other plant groups, like tall herbs and woody plants, have over-topped them. If grazing is sufficiently recurrent this would never happen and grasses would dominate the plant community. The results thus support the idea that the graminoid strategy is superior in dealing with pulsatory grazing, while persistently intense grazing favours plants with low stature (see also Pettersson 1958, McNaughton 1979, Huntly 1987, Oksanen 1990).

## Implications for food-limitation in voles

The preferences found in this experiment correspond to the main patterns found in the literature. *M. agrestis* has a varied diet with grasses and low herbs as the most preferred food items (Hansson 1971a, b, Stenseth et al. 1977). The two *Clethrionomys*-species prefer herbs and eat very little graminoids (Kalela 1957, Hansson 1971a, 1979, 1985), while *L. lemmus* is a specialist on graminoids and mosses (Hansson 1969, Kalela and Koponen 1971). It should be noted that our data refers to cut shoots, rather than ingested. This distinction does not matter for shoot mortality of the plants, but it might make a difference for the animals. Some plant material was left lying on the plots and in the runways, but most biomass seems to have been eaten and we could not find any patterns regarding which species or groups were left uneaten (P. Ekerholm, unpubl.).

One vole individual on 6.75 $m^2$ of vegetated area on each table roughly corresponds to a population density of 1480 individuals per hectare. Population densities in the wild rarely go above 50 animals per ha in peak years for *Clethrionomys* spp., and even for *Microtus* spp. the level of 200 individuals per ha is seldom exceeded (Hansson 1969, Krebs and Myers 1974, Myllymäki 1977, Henttonen et al. 1987). It thus seems highly unlikely that depletion of adequate forage causes summer declines of microtine rodents in nutrient-rich, moist boreal habitats. Our data suggest that, without predation and social interactions, voles can survive at high densities, and that food-limitation in habitats dominated by potential forage plants is accompanied by obvious destruction of the vegetation as seen on islands with abnormal high densities of *M. agrestis* (Pokki 1981) and *C. rufocanus* (Oksanen et al. 1987).

According to the Freeland (1974) hypothesis, vole grazing boosts the competitive position of toxic plants, and the increased relative abundance of toxic species causes the decline of the vole population. The relaxed grazing pressure shifts the competitive balance to the favour of non-toxic species and thus starts a new rise of the voles. In the short run, intense vole grazing did seem to favour toxic herbs over non-toxic ones in our experiment. However, we found no evidence that this impact had been carried over to the next growing season, or that non-toxic herbs would be favoured in the absence of grazing. On the contrary, toxic herbs had their highest biomass on control and lemming plots, both at the end of the treatment (Fig. 3) and one growing season later (Fig. 5). Moreover, toxic species were not consistently avoided. One *C. rufocanus* individual actually preferred the toxic *Actaea spicata* (Table 2) which were hoarded in runways in large amounts and consumed later on.

Another possibility is that the plants themselves become less edible, due to the induction of chemical defences (Haukioja and Hakkala 1975, Rhoades 1985). However, in a study with *C. rufocanus* and *Vaccinium myrtillus* twigs, grazing seemed to improve the food quality (Oksanen et al. 1987). In the single case known to us where vole grazing has been shown to induce the production of defensive chemicals, the impact remained ephemeral and was not carried over to the next growing season (Lindroth and Batzli 1986).

It thus seems extremely unlikely that the poor adult survival observed during the summer declines in the cyclic vole populations of boreal and subarctic Fennoscandia (Henttonen et al. 1977, 1987, Laine and Henttonen 1983, Hansson and Henttonen 1985) could be caused by acute shortage of adequate food. Predation, diseases, parasites, and social factors, alone or in combinations, seem to offer more realistic alternatives.

However, we cannot refute the conjecture that food shortage reduces the reproductive output of voles (Myllymäki 1977) or the quality of female offspring (Hansson 1989) under more reasonable population densities. As the numerical dynamics of a population depends on the balance between reproduction and mortality, our results are compatible with a variant of the "green desert" hypothesis, stating that the reproduction of herbivorous animals is critically dependent on rare, high-quality components of the vegetation. To critically test this variant of the "green desert" hypothesis, one must work on an essentially larger spatial and temporal scale. Such studies have been performed on islands (Pokki 1981, Oksanen et al. 1987) and in field exclosures (Krebs et al. 1973, Boonstra and Krebs 1977, Desy and Batzli 1989 ). So far, the results obtained are as negative to the "green desert" hypothesis as those reported here; enclosed vole populations could reach abnormally high densities and did not decline until the vegetation was clearly destroyed.

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## Appendix

Complete list of marked vascular plant species. The abbreviated names are used in Table 2. The classification into the five growth forms are based on morphological characters. Species with nitrogen-based defence is marked with a star, and species with a carbon-based defence with a plus. The species marked with a star are all highly toxic to animals and man. *Convallaria majalis* contains cardiac glycosides, *Paris quadrifolia* contains glycosides, while the toxicology of *Actaea spicata* is complex and not clearly understood in detail (Kingsburg 1964, Hegnauer 1964–1973, Lewis and Elvin-Lewis 1977). Nomenclature in accordance with Flora Europaea (Tutin et al. 1964–1980).

| Plant species | Abbreviated name | Growth form | Toxic |
|---|---|---|---|
| *Actaea spicata* L. | actaea | T | * |
| *Agrostis capillaris* L. | agrostis | G | |
| *Anthriscus sylvestris* (L.) Hoffm. | anthriscus | L | |
| *Athyrium filix-femina* (L.) Roth. | athyrium | T | |
| *Betula* spp. | betula | W | |
| *Calamagrostis purpurea* (Trin.) Trin. | calamagrostis | G | |
| *Carex digitata* L. | carex dig | R | |
| *Carex vaginata* Tausch. | carex vag | R | |
| *Cicerbita alpina* (L.) Wallr. | cicerbita | T | |
| *Convallaria majalis* L. | convallaria | T | * |
| *Corallorhiza trifida* Chatel. | corallorhiza | L | |
| *Deschampsia cespitosa* (L.) Beauv. | desch cesp | G | |
| *Deschampsia flexuosa* (L.) Trin. | desch flex | G | |
| *Dryopteris assimilis* S. Walker | dryopteris | T | |
| *Epilobium angustifolium* L. | epil ang | T | |
| *Epilobium montanum* L. | epil mon | L | |
| *Equisetum pratense* Ehrh. | equisetum | L | |
| *Festuca rubra* L. | festuca | G | |
| *Fragaria vesca* L. | fragaria | L | |
| *Geranium sylvaticum* L. | geranium | T | |
| *Gymnocarpium dryopteris* (L.) Newm. | gymnocarpium | L | |
| *Hieracium* sp. | hieracium | R | |
| *Linnaea borealis* L. | linnaea | W | |
| *Listera cordata* (L.) R.Br. | listera | L | |
| *Luzula pilosa* (L.) Willd. | luzula | R | |
| *Lycopodium annotinum* L. | lycopodium | W | + |
| *Maianthemum bifolium* (L.) F.W.Schm. | maianthemum | L | |
| *Melampyrum sylvaticum* L. | melampyrum | L | |
| *Melica nutans* L. | melica | G | |
| *Milium effusum* L. | milium | G | |
| *Moneses uniflora* (L.) A.Gray | moneses | L | |
| *Orthilia secunda* (L.) House | orthilia | L | |
| *Oxalis acetosella* L. | oxalis | L | |
| *Paris quadrifolia* L. | paris | T | * |
| *Picea abies* (L.) Karsten | picea | W | + |
| *Poa nemoralis* L. | poa nem | G | |
| *Poa pratensis* L. | poa prat | G | |
| *Populus tremula* L. | populus | W | |
| *Pyrola* spp. | pyrola | L | |
| *Ranunculus* spp. | ranunculus | L | |
| *Rubus idaeus* L. | rubus id | W | |
| *Rubus saxatilis* L. | rubus sax | L | |
| *Rumex acetosella* L. | rumex | L | |
| *Silene dioica* (L.) Clairv. | silene | R | |
| *Solidago virgaurea* L. | solidago | R | |
| *Sorbus aucuparia* L. | sorbus | W | |
| *Taraxacum* sp. | taraxacum | R | |
| *Thelypteris phegopteris* (L.) Sloss. | thelypteris | L | |
| *Trientalis europea* L. | trientalis | L | |
| *Vaccinium myrtillus* L. | vacc myrt | W | |
| *Vaccinium vitis-idaea* L. | vacc vit | W | |
| *Veronica officinalis* L. | veronica | R | |
| *Viola riviniana* Rchb. | viola | L | |

Growth forms: G=grass, L=low herb, R=rosette plant, T=tall herb, W=woody plant.